Systema Porifera: A Guide to the Classification of Sponges, Edited by John N.A. Hooper and Rob W.M. Van Soest

Order Halichondrida Gray, 1867

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Order Halichondrida Gray (Demospongiae) is here employed in the redefined sense of Van Soest *et al*. (1990; with subsequent published adjustments), and includes the former much more restricted Halichondrida and part of the former Axinellida as proposed in earlier classifications (e.g., Lévi, 1973; Bergquist, 1978; Hartman, 1982). The order is defined to include sponges with smooth styles, oxeas or strongyles, occurring often in tandem within the same sponge, but usually without distinct localization, and lacking microscleres other than spined microxeas and raphides. Flexuous, sinuously curved, or contorted megascleres are relatively common. Skeletal architecture is basically plumoreticulate, but in various groups this is modified to dendritic columns of megascleres or confused bundles with many loose single megascleres. Ectosomal skeleton ranging from specialized, tangentially intercrossing or obliquely arranged palisades or bouquets of mega- and microscleres, to absent or undifferentiated, or replaced by thick organic skin, or rarely with sand grains. Five families are recognized, based on features of the ectosomal and choanosomal skeleton. Axinellidae, Bubaridae and Dictyonellidae lack a specialized ectosomal skeleton, whereas Halichondriidae and Desmoxyidae with few exceptions have an ectosomal skeleton consisting of spicules arranged tangentially or in the form of palisades/bouquets. Axinellidae differ from Bubaridae and Dictyonellidae in having a well-developed dense reticulation of megascleres, often showing axial and extra-axial differentiation, and their surface is velvety or microhispid due to projecting choanosomal spicule bundles. Bubaridae are thinly encrusting sponges with monactinal megascleres erect on a basal mass of bent or flexuous diactinal spicules. Dictyonellidae have a fleshy organic skin, and lack a neat reticulation, megascleres usually forming dendritic columns or a vague confused reticulation of styles, rarely oxeas. Desmoxyidae have spined microscleres or smaller megascleres at the surface, either tangentially or perpendicularly arranged. Halichondriidae have only smooth megascleres, and with few exceptions have a tangential crust of intercrossing oxeas, rarely styles. Where known most Halichondrida are oviparous, but *Halichondria*, *Hymeniacidon* (Halichondriidae), *Scopalina* and *Svenzea* (Dictyonellidae) are viviparous; the latter have very large ovoid larvae. Halichondrida are common inhabitants of all marine habitats in all oceans and seas.
Keywords: Porifera; Demospongiae; Halichondrida; Axinellidae; Bubaridae; Dictyonellidae; Desmoxyidae; Halichondriidae.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Halichondriadae Gray, 1867a: 518. Halichondrina Vosmaer, 1887: 335. Axinellides Lévi, 1953a: 3 (in part). Axinellida Lévi, 1957b: 181 (in part). Halichondrides Lévi, 1953a: 3. Clavaxinellides Lévi, 1956a: 167 (in part). Clavaxinellida Lévi, 1957b: 181 (in part). [Claraxinellida] Lévi, 1957b (*lapsus*, p. 183). Halichondriida Wiedenmayer, 1977: 148 *(nomen correctum)*.

Definition

Ceractinomorpha Demospongiae with styles, oxeas, strongyles or intermediate spicules, of widely diverging sizes, and not functionally localized; skeleton plumoreticulate, dendritic or confused; microscleres if present microxeas and/or trichodragmas.

Diagnosis

Encrusting, massive, lobate, digitate, fistular, ramose, tubular or flabellate sponges. Surface smooth, microhispid, conulose or grooved. Ectosomal skeleton consisting of a crust of intercrossing megascleres, or bouquets/palisades of small megascleres c.q. microxeas, but also frequently absent or thickly organic. Choanosomal skeleton basically plumoreticulate, consisting of plumose sheets or bundles of megascleres obliquely or squarely interconnected by shorter plumose bundles; frequently the interconnecting bundles are absent or vaguely developed, resulting in dendritic skeletal columns or entirely confused skeletons. Spongin and interstitial collagen may be present in considerable quantities, also binding the spicule bundles, but may also be vestigial, resulting in lax or crumbly texture. Megascleres styles, oxeas and strongyles, often intergrading into each other with apices ranging from sharply and gradually tapering, to bluntly rounded, often with characteristic stair-stepped appearance. Styles may occasionally have a slightly developed subterminal tyle. The respective megasclere types frequently occur together in a single sponge, but may also be confined to exclusively oxeas or styles; strongyles always occur together with one of the other megasclere types. Diactinal spicules (oxeas, strongyles) in some genera and species may be flexuous, sinuously curved or contorted. Microscleres except trichodragmata are absent, but some genera have the smallest category of oxeas or styles ornamented with spines or, in one genus, disc-like outgrowths; such spicules may be conveniently named microscleres but the homology with true microscleres is debatable.

Scope

Five families are recognized in the order, Axinellidae Carter, 1875, Bubaridae Topsent, 1894, Desmoxyidae Hallmann, 1916, Dictyonellidae Van Soest *et al*., 1990 and Halichondriidae Gray, 1867a. Together they contain many hundreds of species occurring in all marine habitats and in all geographic regions. Axinellidae and Halichondriidae are particularly speciose, Bubaridae and Dictyonellidae are less diverse, with Desmoxyidae intermediate in diversity.

Remarks

The plumoreticulate skeletal architecture may be a synapomorphy for a much wider group of Demospongiae (see Van Soest, 1991). This character is progressively lost in the families Dictyonellidae and Halichondriidae. However, a basic plumorecticulate or plumose architecture is found even in these taxa with few exceptions. Although the combination of styles and oxeas is also found in a few poecilosclerid Microcionina and Myxillina, in these groups they are localized to particular regions and/or have several geometric categories. For instance, in Myxillina stylote choanosomal spicules are combined with ectosomal diactines; in the raspailiid *Echinodictyum* choanosomal oxeas are arranged into tracts which are echinated by (acantho-)styles. Indiscriminate occurrence of styles and oxeas is not found. Localized spicules in *Didiscus, Myrmekioderma* and *Higginsia* are conveniently considered microscleres. Sinuous longer or shorter diactinal spicules are found in various groups distributed throughout the order: e.g., *Axinella cannabina*, *Phakellia*, *Auletta* (Axinellidae), *Bubaris* (Bubaridae), *Acanthella, Dactylella* (Dictyonellidae), some *Axinyssa* and some *Topsentia* (Halichondriidae). This distribution may be interpreted as retention of ancestral spicules, possibly related to 'lithistid' spicules, through *Monocrepidium* (Bubaridae) and fossil genera such as *Cephalorhaphidites* and *Megaloraphium*, and thus constitute an underlying synapomorphy of the order.

Taxonomic history

Gray (1867a: 518) erected a family Halichondriadae which contained a mixture of Haplosclerida, Poecilosclerida and Hadromerida, and indeed included Halichondriidae. Later Vosmaer (1887: 335) used the suborder name Halichondrina for a similarly wide group of Ceractinomorpha (dubbed Cornacuspongida by him), basically only excluding the 'Keratosa'. Ridley & Dendy (1887: lviii) employed a suborder Halichondrina in the order Monaxonida Sollas, 1883, which covered the same groups. Halichondrida were narrowed down by Topsent (1928c: 37) to a group of four families (Axinellidae, Astraxinellidae, Bubaridae, and Heteroxyida), which together cover most of the present concept of Halichondrida. Remarkably, the family Halichondriidae was merged with Axinellidae, and some genera now considered Halichondriidae like *Spongosorites*, were excluded. The most important difference with present content of Halichondrida is the inclusion of Astraxinellidae (=Hemiasterellidae), which are here considered to belong to Hadromerida on account of the possession of asters. De Laubenfels (1936a) distributed the latter group over several orders and families, and retained the remaining groups in a Halichondrida of five (the apparently preferred number of this author) families: Axinellidae, Halichondriidae, a new family Hymeniacidonidae (containing in addition to *Hymeniacidon*, many genera now united in Dictyonellidae), a new family Semisuberitidae (containing an odd assemblage of poecilosclerid and haplosclerid genera), and a new family Monanthidae (for 'sublithistid' genera). By this subsequent building on previous classification schemes, and by increasing the focus of the group by removing outlying families and genera, a continuity and consensus was achieved, which allowed some form of stable use of the classification. This stability was significantly disrupted by new, non-skeletal evidence produced by Lévi (e.g., 1951, 1953a, 1956a, 1957b and following). This author, after a long and careful study of sponges in the field, giving him access to previously unknown life cycle information, discovered broad group-related modes of reproduction. In large groups of sponges, like tetractinellids and hadromerids, all species investigated were found to be oviparous, whereas other groups, like haplosclerids, poecilosclerids and 'keratose' sponges appeared to be always brooding their larvae. He later proposed (Lévi, 1953a, 1956a, 1957b) to subdivide the Demospongiae in two subclasses, which were based on ovipary (Tetractinomorpha) and vivipary (Ceractinomorpha). Lévi (l.c.) demonstrated that within the Halichondrida some families were oviparous (Axinellidae *sensu* de Laubenfels, 1936a), other families were viviparous (Halichondriidae *sensu* de Laubenfels). This led him to propose a subdivision of the group, with orders Axinellida (families Axinellidae, Bubaridae, Desmoxyidae, Euryponidae, Hemiasterellidae, Raspailiidae, Rhabderemiidae, Sigmaxinellidae and Trachycladidae), assigned to Tetractinomorpha, and Halichondrida *s.s*. (families Halichondriidae and Hymeniacidonidae) assigned to Ceractinomorpha. Axinellida was further underbuilt by emphasizing the frequent occurrence of axially condensed skeletons in members of this group (see Lévi, 1973 for a comprehensive treatment). The combination of axial skeletons and asters in Hemiasterellidae and axial skeletons and spinispirae in Trachycladidae led Lévi (1956a: 167) to propose a formal higher taxon including both Hadromerida and Axinellida, the superorder Clavaxinellides, which he later (Lévi, 1957b: 181) corrected to Clavaxinellida (and misspelled as Claraxinellida on p. 183). These combined proposals were received with approval by most contemporary authors (e.g., Vacelet, 1969; Bergquist, 1978; Hartman, 1982), and much effort was directed towards obtaining additional support for this scheme. From 1985 onwards, again the consensus over these groups was broken, by independent studies of Hooper (1990b) on the relationship of oviparous ('tetractinomorph') Raspailiidae and viviparous ('ceractinomorph') Microcionidae, and Van Soest *et al*. (1990) and Van Soest (1987a, 1991) on the relationships of Axinellidae and Halichondriidae. Criticism of the Lévi system amounted to the conclusion that too much emphasis was placed on only a few characters and conflicting character distributions were ignored. These heavy-weight characters (vivipary, axial condensation of the choanosomal skeleton) were moreover given as much weight for their presence as for their (primitive) absence, a philosophically unsound character treatment: one cannot define a group of organisms on the fact that it does not possess a certain feature, unless one assumes it was lost. Both Hooper (l.c.) and Van Soest (l.c.) brought forward contrasting evidence and the latter suggested to abandon the (Clav-)Axinellida *sensu* Lévi, in favour of a more conservative classification. Halichondrida *sensu* Topsent and de Laubenfels, with necessary emendations, containing core families Axinellidae and Halichondriidae, along with Bubaridae, Dictyonellidae and Desmoxyidae, fit better with the available morphological characters. An initial 28S rRNA sequence analysis performed with a 27 species sample (Alvarez *et al*., 2000a) generally confirmed the likely close relationships of these families. Chemosystematic evidence (Van Soest & Braekman, 1999) also points at close relationships with two families of compounds (pyrrole-2-carboxylic derivatives and cyanoditerpene-derivatives) distributed over species and genera of Axinellidae, Bubaridae, Dictyonellidae and Halichondriidae. The pyrroles also occur in Agelasida (in both families Agelasidae and Astroscleridae), which may be evidence along with 28S rRNA sequence data (Chombard *et al*., 1997) to support a possible future merger of Agelasida and (part of) Halichondrida. An abstract of a study by Chombard *et al*. (1999) reports the finding of 28S rRNA

sequence similarity between Suberitidae, Polymastiidae and Halichondriidae, resulting even in a proposal for a new suborder Suberitina comprising these families, to be assigned to Hadromerida. Whereas such studies and results indicate that the present concept of Halichondrida may be subject to future change, it is premature to follow suggestions such as a merger of Agelasida and (parts of) Halichondrida, or a merger of Hadromerida and (parts of) Halichondrida. Future studies with larger samples of representative taxa and using more than a single gene are necessary to enable confirmation or refutation of the present concept, which is based on morphological analysis of all type specimens and species and a large sample of additional species.

KEY TO FAMILIES

(1) Ectosomal specialization present, either in the form of a tangential crust or single spicule layer, a palisade of smaller and/or larger megascleres or erect or scattered microscleres; surface smooth, but may be wrinkled or thrown up into folds and depressions 2
No ectosomal specialization, surface velvety, or hispid due to single projecting spicules, or fleshy-organic, without tangential spicules 3

(2) At the surface there is a tangential layer or a palisade of spiny smaller oxeas or strongyles ..... **Desmoxyidae**
No spiny megascleres or microscleres; surface skeleton consists either of a tangential crust or tangential single spicules, or palisades c.q. bouquets of smaller spicules mingled with larger choanosomal spicules ..... **Halichondriidae**

(3) Surface velvety or hispid, due to projecting single spicules or choanosomal spicule tracts; sponges firmly resilient 4
Surface fleshy-conulose, with organic skin thrown up into conules by choanosomal fibres or spicules; comes off in flakes when attempted to obtain a surface peel ..... **Dictyonellidae**

(4) Thinly encrusting, not exceeding 1 cm thickness, strongly hispid, due to erect monactinal megascleres, with heads embedded in a basal layer of interlacing megascleres ..... **Bubaridae**
Elaborate growth forms; surface microhispid, often velvety 5

(5) Choanosomal skeleton reticulate, often with axial and extra-axial differentiation ..... **Axinellidae**
Choanosomal skeleton confused ..... **Halichondriidae (genus *Axinyssa*)**